AGE AND SEX DIFFERENCES IN MOLT OF THE MONTAGU'S HARRIER

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Abstract.—Age and sex differences in the timing and pattern of feather molt in Montagu's harrier (*Circus pygargus*) was studied in 184 museum specimens and live birds collected throughout their breeding and wintering ranges. Molt in adults lasted 6–8 mo, starting in May–June in the breeding areas and finishing in January–February on the wintering grounds. Apparently, Montagu's harriers do not suspend molt during migration. Molt of primaries started earlier in adult females than in adult males, which was probably related to their different roles in feeding nestlings during the breeding season, but both sexes finished molt at about the same time. Yearlings started body molt on the wintering grounds and there was a considerable discrepancy in the extent of body molt of yearlings between data obtained from skins and those from live birds. Yearlings attained plumage similar to that of adults after the first complete molt. Timing of flight feather molt in yearlings and second-yr males was similar to that of adults even though they were not engaged in reproduction. Nevertheless, they finished molting earlier than older birds, but this difference was not significant.

Key Words: *Age and sex differences*; Circus pygargus; *Montagu's harrier*; *molt phenology*; *molt rate.*

Diferencias en la muda del aguilucho cerizo con respecto a la edad y al sexo

Resumen.—Se ha estudiado el patrón de muda en 184 aguiluchos cenizos (*Circus pygargus*) (fundamentalmente ejemplares en museos, y algunos individuos vivos), procedentes de todo su rango de distribución, y se analizan las diferencias en fenología de muda debidas a la edad y al sexo. La muda en los adultos dura 6–8 meses, comenzando en mayo–junio en las zonas de cría, y terminando en enero–febrero en los cuarteles de invernada. Los datos disponibles sugieren que los aguiluchos cenizos no suspenden la muda durante la migración. La muda de las primarias comienza antes en las hembras adultas que en los machos adultos, lo que probablemente está relacionado con la diferente contribución de los sexos a la alimentación de los pollos, pero ambos sexos terminan más o menos al mismo tiempo. Los individuos de primer año comienzan la muda corporal en las áreas de invernada. Encontramos divergencias importantes en el grado de muda corporal de los individuos de primer año, entre los datos procedentes de ejemplares de museo y datos procedentes de observaciones de campo. Se discuten las posibles razones de esta divergencia. Al final de la primera muda completa, los individuos de primer año adquieren un plumaje similar al de los adultos. El comienzo de la muda en los individuos de primer año y en los machos de segundo año es similar a la de los adultos, aunque estos grupos de edad no se reproducen. Sin embargo, parecen terminar la muda antes que los individuos de más edad, aunque las diferencias no son significativas.

[Traducción de author]

Feather molt, reproduction, and migration are three of the more energetically costly components of avian life history. Molt is usually timed to minimize peaks in energy demands during either reproduction or migration, and the duration and extent of molt is constrained by the energy invested in either of the latter two factors (Pietianen et al. 1984). If there are differences between the sexes in their relative contributions towards breeding, they may be reflected in sexual differences in molt. Likewise, age-related differences in molt may be expected between individuals that have not yet entered the breeding population, and this should be especially prominent in long-lived species with delayed sexual maturation.

Relatively little is known about molt in diurnal birds of prey, when compared with that of other bird orders. Large raptors such as eagles and vultures do not undergo a complete molt every year,

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but have several foci in the primaries where primaries are molted sequentially (Stresemann and Stresemann 1966, Houston 1975, Edelstam 1984, Bortolotti and Honeyman 1985). In so doing, they avoid excessive raggedness in the wings, which would impair the lift necessary for flight. In contrast, small accipitrids such as hawks usually have one complete molt a year, replacing the primaries from the innermost to the outermost feathers, and the secondaries from three foci (Miller 1941, Piechocki 1955, Stresemann and Stresemann 1966).

The Montagu's harrier (*Circus pygargus*) breeds throughout Europe (wintering in Africa) and the Asian/Russian steppes (in the Indian subcontinent). The molt of Montagu's harrier has never been previously described in detail. Here, we use museum skins (collected throughout its range) and field data from Madrid (Spain) and Sénégal (Africa) to describe the patterns of molt in this species, the differences in timing and duration of molt between males and females, and the acquisition of adult body and flight feathers by yearlings.

METHODS

Sources of Data. Data were recorded from 166 specimens from the Natural History Museum, Tring, UK (28 female yearlings, 31 male yearlings, 36 adult females, 71 adult males), 10 skins from the Museum of Natural History, Madrid (three adult females, seven adult males), three skins of adult males from the Collection Hagi Botti, OR-STOM Station, M'bour, Sénégal, and five breeding birds trapped alive in Madrid (two adult males, three adult females).

Field observations of yearlings in breeding areas in Spain were also used for comparison. All yearlings could be identified by the presence of uniformly dark secondaries characteristic of juvenile Montagu's harriers. Males change their iris color from brown to uniformly pale yellow before they are 3–4 mo old. Females do not attain yellow irides until they are 3–4 yr old, although they might have various degrees of yellow spotting before that. We used eye color to sex birds in juvenile plumage when possible.

Molt Scores. Molt of individual remiges and rectrices was scored from 0–5, following Ginn and Melville (1983), where 0 represents an old feather, and 5 a fully-grown, new feather. The intermediate values (1–4) represent progressions of feather growth. Throughout this study, primaries are numbered from 1 (the innermost) to 10 (the outermost), and the secondaries, including the tertials, are numbered from 1–13 (1 being the outermost). Molt for the vestigial outermost primary (P11) was not recorded. A Primary Molt Score (PMS) was calculated for each bird as the sum of the molt scores of the 10 primaries in one wing, and PMS ranged from 0–50 (Ginn and Melville 1983). When the PMS differed between wings of the same bird, an average of the two scores was

used in analyses. Similarly, we calculated a Secondary Molt Score (SMS, range 0–65), and a Tail Molt Score (TMS, range 0–30) for each bird.

We determined the order in which secondary feathers or tail feathers were molted by calculating the accumulated scores for each numbered feather and ranking each according to its accumulated score. Variations between wings in the order of secondary molt were recorded, but the total score was not significantly different between wings (Mann-Whitney; $W_{120,120} = 14475$, $P = 0.97$). Molt of tail feathers was nearly always symmetrical. Thus, we combined values from both sides for each individual. Primaries were molted sequentially, so we did not calculate accumulated scores for them.

The extent of body molt in yearlings was categorized for each body tract (head, mantle, coverts, breast, and belly) on a four-point scale: 0 (no molt), 1 (very few new feathers present), 2 (mixed new and old feathers), and 3 (molt finished or nearly finished).

Raggedness Scores. An index of raggedness (Haukioja 1971) was calculated for each feather tract (primaries, secondaries, and tail), using the sum of values in each feather of the tract. Each feather was scored with values ranging from 0–4 according to their molt score, where 0 indicated a feather of full length (whether old or new), 4 indicates a feather at the first stage of growth (molt score 1), 3 a feather with molt score 2, 2 a feather with molt score 3, and 1 a feather with molt score 4. For each individual, the sum of raggedness scores from both sides (left and right) of each tract was used as an overall index of raggedness.

Data Analysis. Differences in the molt scores between males and females and age classes were analyzed with nonparametric statistics (Mann-Whitney test). Variations in the timing of secondary molt related to primary molt were analyzed with linear, parametric analysis.

Since several of the skins were dated only to month and not to day of capture, we analyzed data by month. This helped to account for latitudinal differences in phenology between birds coming from different regions because breeding phenology in the Montagu's harrier varies on average less than a month between southern and northern Europe (Arroyo 1995). Initially, data for birds from Europe (west of Ural mountains) and data for birds that had been collected in India (presumed to breed in the central Asian steppes) were analyzed separately. This avoided potential differences in phenology between both areas, since no data on timing of breeding for the Asian populations of Montagu's harrier were available. No significant differences in molt scores were found between birds from both regions for equivalent months (Mann-Whitney; $W_{21,10} = 319.0$, $P = 0.47$), so they were combined for subsequent analyses.

RESULTS

Molt in Adults. Adult males and females started molting on the breeding grounds in May–June, and finished molting on the wintering grounds in January–February (Fig. 1). Primary molt was completed in 6–8 mo. Females started molting primaries before males, but both sexes finished at about
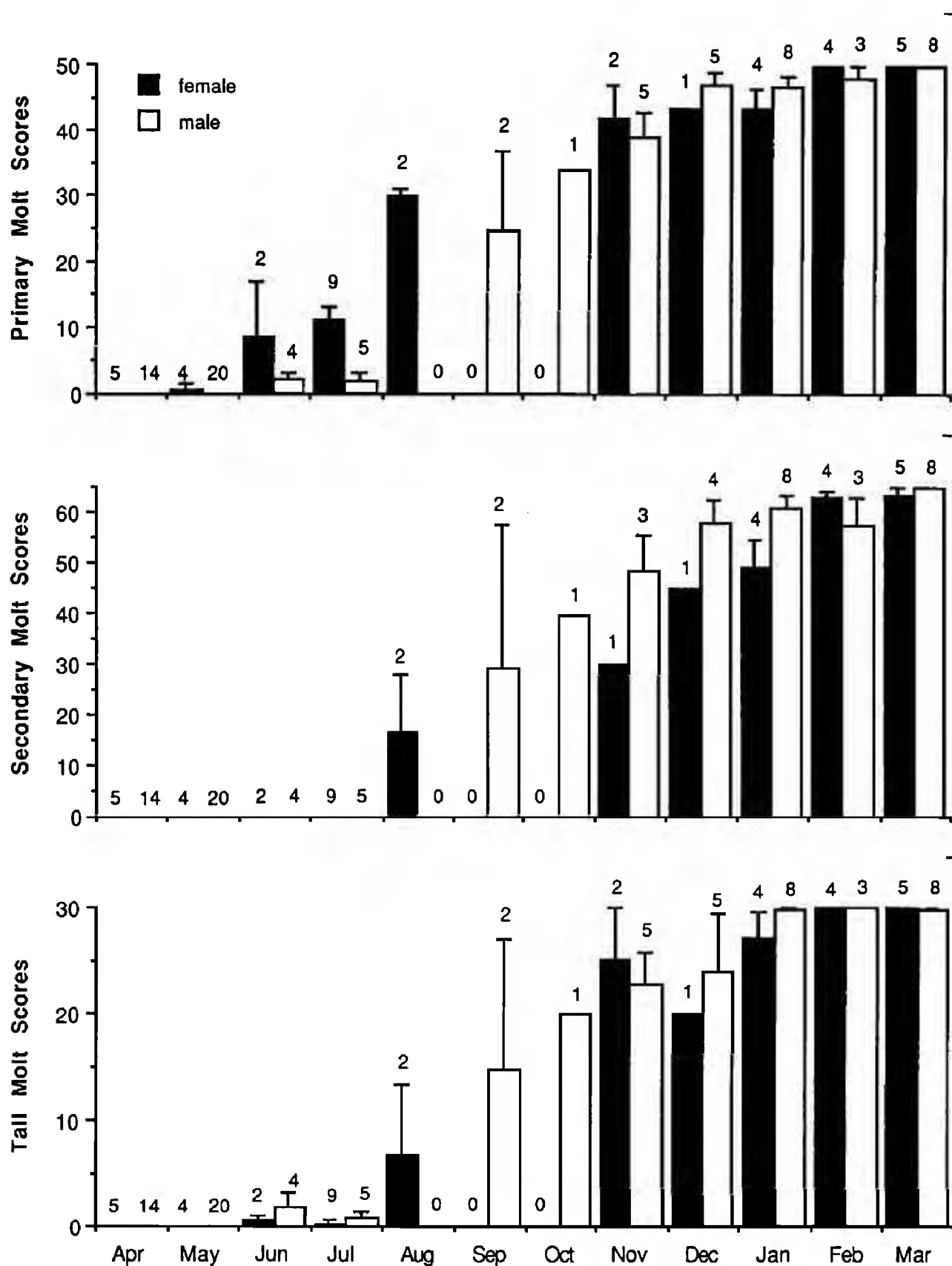
Figure 1. Molt phenology of flight feathers in adult Montagu's harriers. Histograms represent the mean (±SE) primary, secondary and tail molt scores throughout the year for both males and females. Sample size (number of individuals) is given above the histograms.

the same time (Fig. 1). The mean PMS for the breeding months (April–July) was significantly lower in males than in females (Mann-Whitney; $W_{20,43}$ = 816.5, P = 0.0009), but the means were similar in November–February (Mann-Whitney; $W_{11,21}$ = 185.5, P = 0.88). Accordingly, the slope of the regression of PMS vs month was higher for males (5.36) than for females (5.01).

Both males and females started molting secondaries in August–September, and finished at the same time that primary molt finished (Fig. 1). Males started molting secondaries at a significantly earlier stage of primary molt than females did (GLM SMS = PMS + Sex; $F_{1,117}$ = 1956.5, P = 0.0001 for PMS; $F_{1,117}$ = 12.60, P = 0.001 for Sex; Fig. 2). The pattern of secondary molt was highly
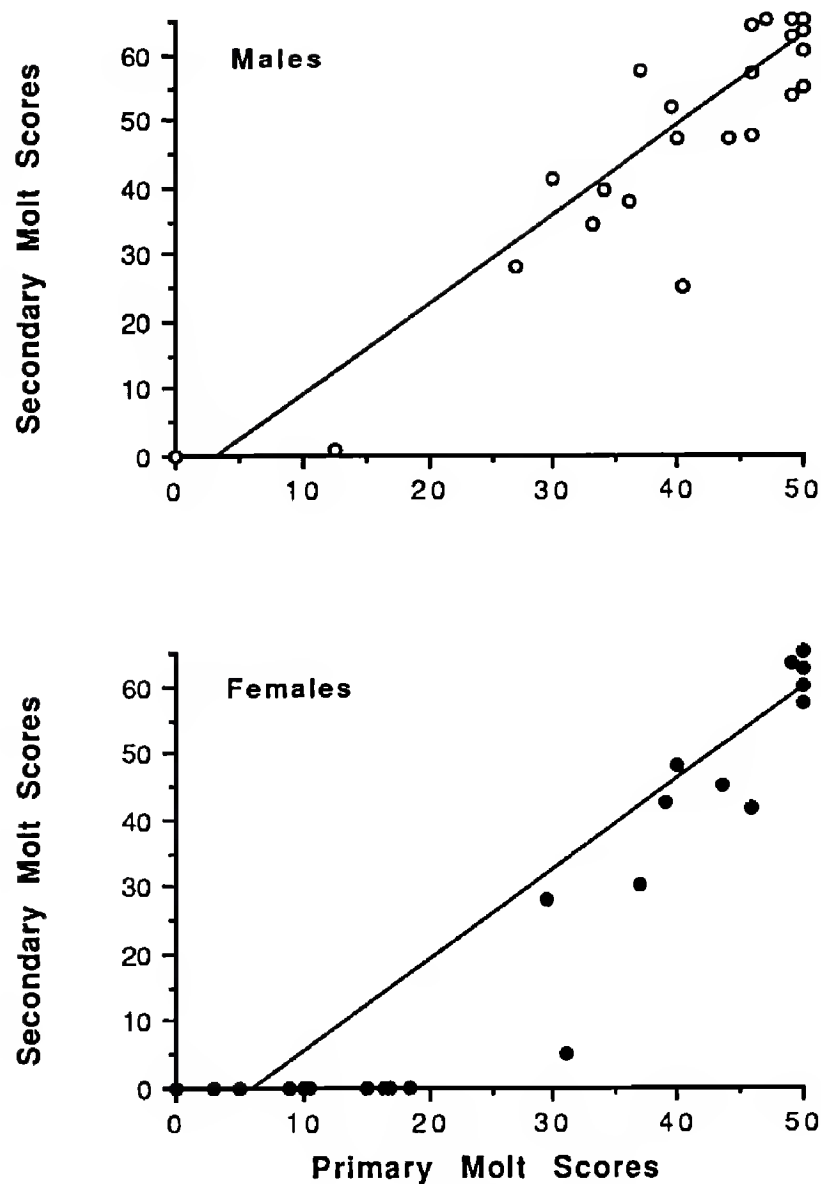
Figure 2. Onset of secondary molt in relation to molt of primary feathers: correlation between secondary molt scores and primary molt scores in adult male ($N = 79$) and female ($N = 40$) Montagu's harriers.

Figure 3. Onset of tail molt in relation to molt of primary feathers: correlation between tail molt scores and primary molt scores in adult male ($N = 79$) and female ($N = 40$) Montagu's harriers.

variable among individuals in relation to the order in which feathers were replaced. The relative order of the accumulated molt scores of each feather (all birds combined) was as follows: for females ($N = 40$): S1 (accumulated score = 180), S5/S11 (165), S2/S13 (160), S4 (155), S12 (150), S10 (146), S9 (130), S3 (123), S6 (120), S7 (115), S8 (108); for males ($N = 79$): S1 (319), S5/S12 (315), S11 (308), S13 (307), S2 (302), S10 (295), S9 (291), S4 (272), S3 (250), S6 (242), S7 (220), S8 (218). These results indicated that two molt foci existed at S1 and S5, and molt at both foci started nearly simultaneously. Another molt center was located in the tertials (S11–13), which were molted at the time, or shortly after the outer secondaries had started to molt. Males seemed to molt the tertials as soon as molt in the outer secondaries had started, while females seemed to molt them more slowly. The order in which tertials were molted did not seem to
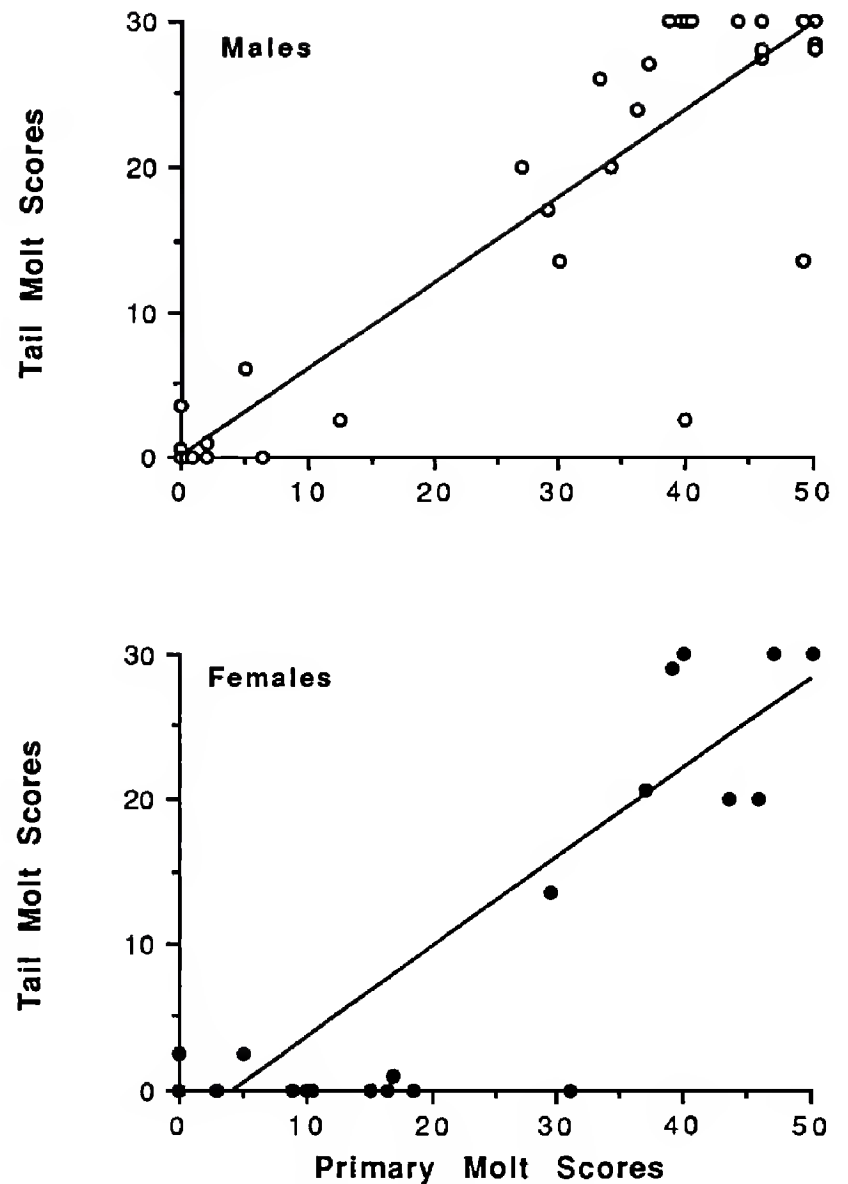
follow a fixed pattern. In general, molt was ascendant from S1 and S11 (the outermost tertial), and appeared to be centrifugal from S5. Data from D. Forsman (in litt.) suggests that molt from S5 is ascendant, given that he found S4 to be one of the last secondaries to be molted. However, we found S4 to be one of the earlier molted secondaries in females and it was not the last secondary to be molted by males.

Molt of tail feathers started about June and finished about January (Fig. 1). As with secondaries, males started molting tail feathers at a significantly earlier stage of primary molt than did females (GLM TMS = PMS + Sex; $F_{1,119} = 1268.6$, $P = 0.0001$ for PMS; $F_{1,119} = 8.15$, $P = 0.005$ for Sex; Fig. 3). The order in which feathers were molted was, as with secondaries, variable but a general pattern was clear from the accumulated molt scores. Molt of tail feathers in females usually started with

the central pair (accumulated molt score of 175), followed by the fourth (166), sixth (161), third (156), fifth (148) and, finally, the second (132) (N = 40). Males had a similar molt pattern, but the sixth pair was the first one to be replaced. The relative order was thus T6 (accumulated score 332), T1 (328), T4 (316), T3 (314), T5 (308) and T2 (294). As in the primaries and secondaries, tail molt seemed to occur more rapidly in males than in females, and the variation in values of accumulated TMS among feathers was lower in males than females. The difference between the highest and the lowest accumulated score was 12% in males and 30% in females which suggested that males molted a greater number of tail feathers at any one time than females.

Primary feathers were most ragged between November–January among females and in June among males. Degree of raggedness in secondaries and tail feathers was generally low throughout the molt cycle in both sexes (Fig. 4). On average, males had higher values of raggedness for all flight feather tracts than females, but differences between the sexes were not statistically significant (Mann-Whitney; $W_{40,80}$ = 2598.5, 2365.0 and 2321.5, P = 0.82, 0.65 and 0.23 for primaries, secondaries, and tail feathers, respectively). The accumulated score of raggedness for all tracts combined peaked for males at values ranging from 23–32 in September–October, while values for females peaked at 25 in November. However, no data existed for females for September and October.

Molt in Yearlings. We recorded no body molt in birds collected in October or November, although sample size was small (N = 3). A small percentage of birds of both sexes started body molt in December, usually in the region of the crop, and males also on the rump (Table 1). Central tail feathers were also replaced in about 25% of birds of both sexes. However, the extent of molt completed before spring migration was limited in both sexes. The proportion of yearlings with some degree of body molt increased throughout the spring and summer. Although a few yearlings had not started molting any body feather tracts by July or August, many started but had not completed molt in most tracts by that time. Yearling males that attempted to breed in Madrid were at the same stage of molt as those that did not breed (B. Arroyo unpubl. data). Furthermore, a yearling male that bred in 1994 had molted only the central tail feathers and part of the feathers in the region of the crop when

it arrived on the breeding grounds in Spain. Body molt of yearlings finished in October–November. Males retained some juvenile feathers in the ear coverts and in the nape, which allowed aging of second-year individuals in the hand.

There was a considerable discrepancy between the extent of body molt in yearlings recorded during field observations and from museum specimens. Detailed plumage observations of 30 yearlings (21 males and nine females) were made in breeding areas in Spain. Yearling males showed more advanced body molt than did museum specimens collected at the same time of year and for birds observed in the field, the head, breast and belly tracts, respectively, showed evidence of molt in 91%, 62% and 62% of individuals, compared to 43%, 29% and 14% of museum specimens (Table 1). The extent of molt recorded was also greater for individuals observed in the field. In contrast, yearling females observed in the field showed less advanced body molt than museum specimens. Only 33% of the females observed in the field showed molting in the crop, breast, and belly, compared to over 63% of the museum specimens (Table 1). This discrepancy might be an artifact of the relatively small number of specimens of yearlings, but it may well be a consequence of the relative visibility of newly-molted, grey plumage in yearling males, leading to overestimation of the extent of molt when recorded in the field. In the latter case, the similarity between old and new plumage in females would lead to an underestimation of the extent of body molt in that sex. Furthermore, yearling males showing little or no molt may have been misidentified as females in the field, or more likely, left unsexed due to apparently conflicting characters such as small size but no visible male plumage features.

Primary molt in yearlings apparently started at the same time as that of adults (Fig. 5) and molt scores were similar between both age groups in April–July (Mann-Whitney; $W_{20,12}$ = 194.5, P = 0.90 for females; $W_{43,10}$ = 284.0, P = 0.64 for males). The completion of primary molt in October–February also appeared to be similar for yearlings and adults, however sample sizes were very small for the yearling group (Mann-Whitney; $W_{22,4}$ = 57.5, P = 0.83 for males; insufficient data for females to allow statistical analysis).

Molt of secondary and tail feathers followed the same pattern, and occurred at the same time in relation to primary molt, as in adults. Juvenile
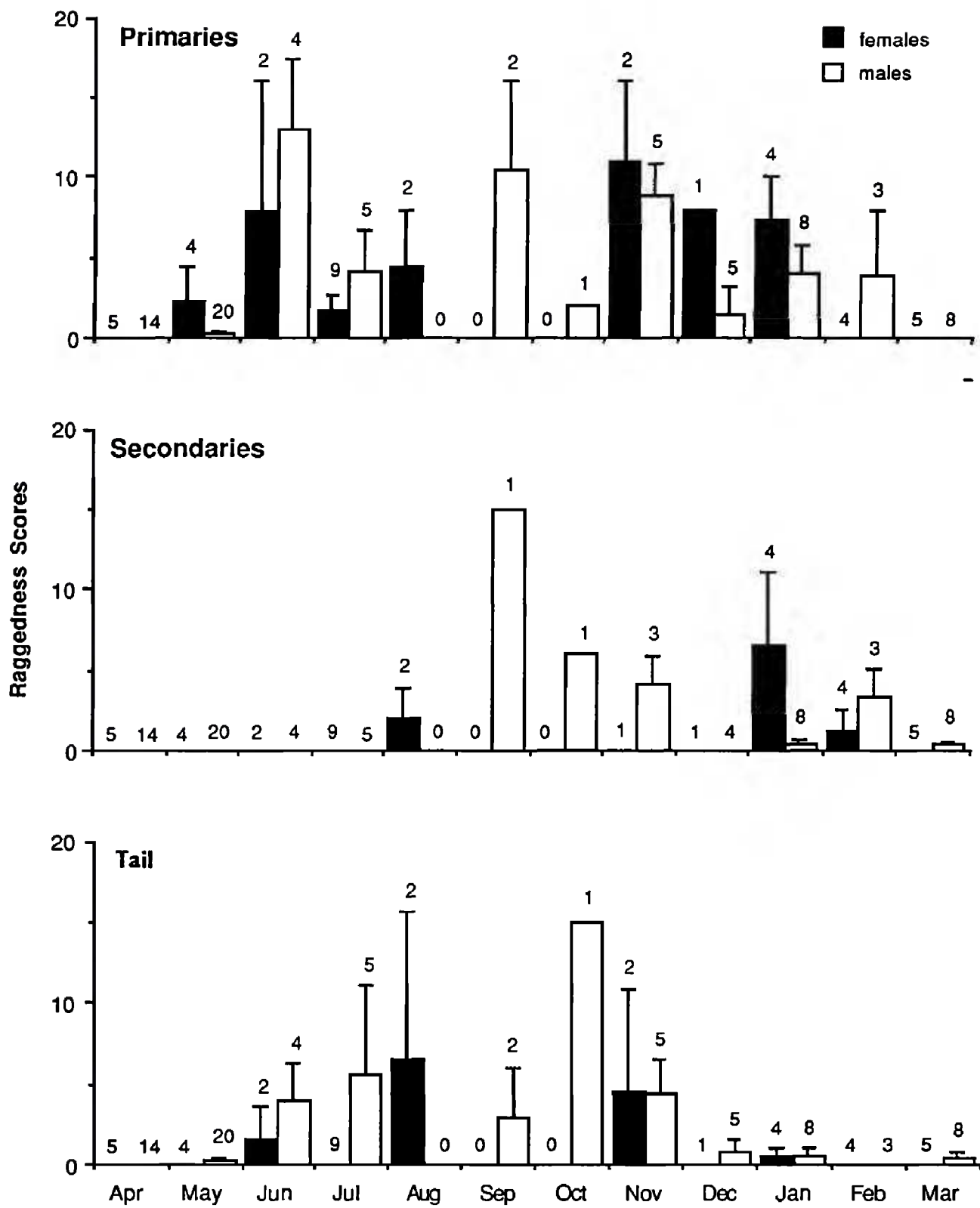
Figure 4. Degree of raggedness in flight feather tracts throughout the year in adult Montagu's harriers of both sexes. Histograms represent the mean (±SE) raggedness scores for primaries, secondaries and tail feathers. Sample size (number of individuals) is given above the histograms.

feathers were replaced by feathers similar to those of adults, only slightly darker. Thus, after the first complete molt, yearlings were indistinguishable from older birds in the field as confirmed by observations of dark-looking plumage in known-age wing-tagged individuals ≥3 years old.

Molt in Second Year Males. Fourteen males in adult plumage could be identified as second-yr males by the presence of a few unmolted, juvenile

feathers on the nape or ear coverts. Second-yr males started molt at the same time as older males, and from May–July the scores for the two age-classes were similar (Mann-Whitney; $W_{34,9} = 231.0$, $P = 0.13$). However, in November–February, second-yr males had higher PMS than older males, and the difference approached significance (Mann-Whitney; $W_{16,4} = 60.5$, $P = 0.08$). Similarly, second-yr males had higher values of SMS than older males

Table 1. Percentage of yearling specimens of Montagu's harriers in which molted feathers were present in different feather tracts. Figures in brackets show the mean score of the individuals in molt (1 [only a few feathers]–3 [molt complete]). N = number of individuals; LC, MC, GC = lesser, middle, and greater coverts, respectively; CTF = central tail feathers; OTF = other tail feathers.

DATE	N	HEAD	CROP	BREAST	BELLY	LC/MC	GC	MANTLE	RUMP	CTF	OTF
Males											
Dec–Jan	9	0	33.3	22.2	0	11.1	0	0	33.3	11.1	0
			(3.0)	(2.0)		(2.0)			(3.0)	(2.0)	
Feb–Mar	3	33.3	66.6	0	0	0	0	0	66.6	0	0
		(1.0)	(1.0)						(3.0)		
Apr–May	7	42.8	85.7	28.6	14.3	42.8	14.3	28.6	57.1	57.1	14.3
		(1.3)	(1.8)	(1.5)	(2.0)	(2.0)	(1.0)	(1.5)	(2.0)	(3.0)	(2.0)
Jun–Jul	3	66.6	100	66.6	33.3	0	0	0	66.6	100	66.6
		(1.0)	(2.0)	(2.0)	(1.0)				(1.5)	(2.0)	(2.0)
Aug	2	50.0	50.0	100	100	100	100	50.0	100	50.0	50.0
		(1.0)	(3.0)	(2.5)	(2.0)	(1.5)	(2.5)	(1.0)	(3.0)	(3.0)	(2.0)
Females											
Dec–Jan	6	0	16.7	16.7	16.7	0	0	0	0	50.0	0
			(2.0)	(2.0)	(2.0)					(2.7)	
Feb–Mar	5	0	40.0	40.0	20.0	0	0	0	20.0	20.0	20.0
			(1.0)	(1.0)	(1.0)				(3.0)	(3.0)	(2.0)
Apr–May	8	37.5	87.5	62.5	62.5	25.0	0	0	25.0	37.5	0
		(2.0)	(1.8)	(1.5)	(2.2)	(1.5)			(1.0)	(3.0)	
Jun–Jul	3	66.6	100	66.6	66.6	66.6	33.3	0	66.6	100	100
		(1.5)	(2.6)	(2.5)	(2.5)	(2.5)	(3.0)		(1.5)	(2.0)	(2.0)

during same period, although the difference was not significant (Mann-Whitney; $W_{15,4}$ = 55.0, P = 0.14), perhaps due to small sample sizes.

DISCUSSION

Molt started in the breeding season (June–July) and finished during the winter months approxi-

mately 6–8 mo later, indicating that the molt period in Montagu's harrier is long compared to that of nonmigratory raptors of comparable body size such as northern goshawks (*Accipiter gentilis*; Reading 1990), sparrowhawks (*Accipiter nisus*; Newton and Marquiss 1982), and little banded goshawks (*Accipiter brevipes*; Schmitt et al. 1981). We could
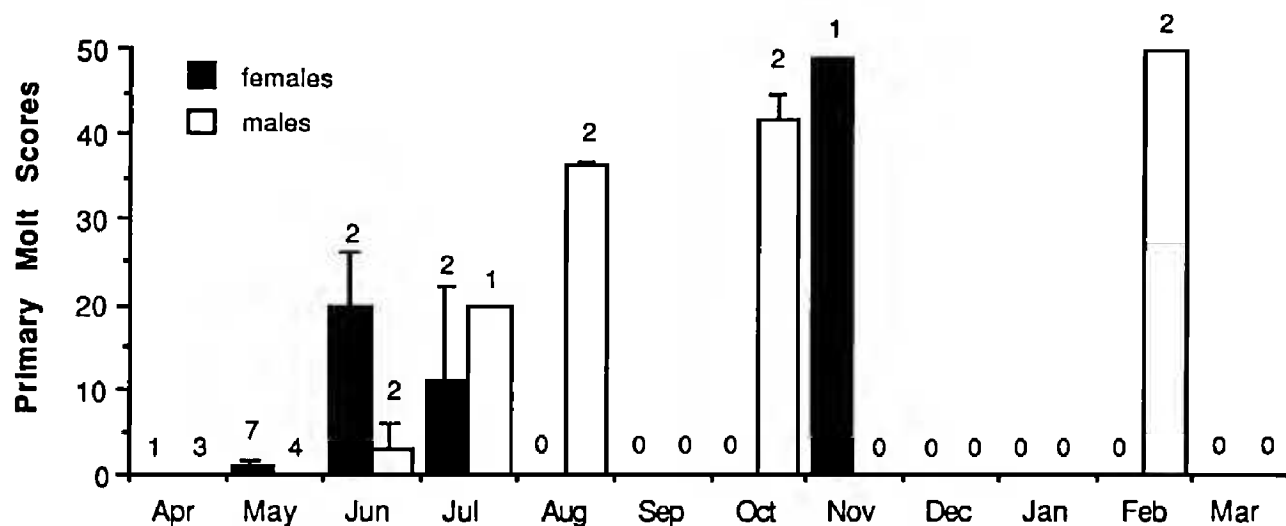

Figure 5. Molt phenology of primary feathers in yearling Montagu's harriers. Histograms represent the mean (± SE) primary molt scores throughout the year for both males and females. Sample size (number of individuals) is given above the histograms. Secondaries and tail feathers, as in adults, are molted in the interval when primaries are molted.

not confirm that birds suspended molt during the migration, as no birds were collected on the migratory route. However, molt scores of birds collected in August–October in either breeding or wintering areas together with high molt scores of the birds collected in November on the wintering grounds, suggested that at least some birds continued to molt while migrating. The duration of the autumn migration is unknown, but may be in excess of 1 mo given the average dates of departure from the breeding grounds (Studinka 1941, Petrement 1968, Perez Chiscano and Fernandez Cruz 1971, Kjellen 1992, Martelli and Parodi 1992, Arroyo 1995), and dates of arrival in wintering areas (Morel and Roux 1966). Migratory flight of harriers seems to be slow and generally at relatively low altitudes. They combine flapping and gliding and hunting along the way (Brown 1976, Ali and Ripley 1978). This mode of migration may allow harriers to continue molting slowly while migrating as they are not soaring birds, for which gaps in the wings would represent higher energetic costs. Piechocki (1955) observed molt in a single captive pallid harrier (*Circus macrourus*). Each tail feather took 45 d to grow completely. Presumably, the primaries would take longer to grow especially from P5 onwards. If single primaries are not shed until growth of the previous one is nearly finished, harriers may keep molting at a slow rate during the migration instead of suspending molt.

As in goshawks and sparrowhawks (Newton and Marquiss 1982, Reading 1990), molt of primaries in Montagu's harrier was spread throughout the entire molt cycle. Secondaries were molted later in the season, but finished at approximately the same time as the primaries. In raptors, molt of secondaries and especially of tail feathers, occurs more quickly than that of primaries (Newton and Marquiss 1985, Underhill 1986, Schmitt et al. 1987). In the Montagu's harrier, molt of the secondaries either did not start, or was not apparently advanced before autumn migration. Secondaries provide much of the lift required for flight (Newton and Marquiss 1982), so it may be especially important to minimize gaps in these feathers for long-distance migration. In accordance with this hypothesis, raggedness scores in the secondaries were always low in comparison with those of primaries.

Males started molting later than females. A similar temporal difference in the onset of molt between sexes has also been documented in sparrowhawks (Newton and Marquiss 1982) and northern

harriers (*Circus cyaneus hudsonius*; Schmutz and Schmutz 1975). Breeding birds must divide their energy between two energetically costly tasks: breeding and molting. In Ural owls (*Strix uralensis*), breeding delays molt and the number of molted feathers is inversely related to energy expended during the previous breeding season (Pietiainen et al. 1984). Therefore, in species in which males do most of the hunting in the breeding season, a sexual dimorphism of molt initiation is expected. In Montagu's harrier, females contributed less than 15% to the feeding of nestlings and fledglings (Arroyo 1995). Females can start molting during incubation, when their energy expenditure is less than that of hunting males. The onset of molt in female sparrowhawks was related to the date they started laying (Newton and Marquiss 1982), but such a relationship was not found in northern harriers (Schmutz and Schmutz 1975) or Swainson's (*Buteo swainsoni*) or ferruginous (*B. regalis*) hawks (Schmutz 1992). Most female Montagu's harriers observed in Madrid appeared to have started molt soon after incubation began (B. Arroyo unpubl. data), but it is not known whether the timing of molt was correlated with timing of egg laying.

As in the northern harriers (Schmutz and Schmutz 1975), male Montagu's harriers apparently molted at a faster rate than females. Female feathers are longer (Nieboer 1973), and may take slightly more time to reach their full length. However, in sparrowhawks in which sexual dimorphism is much greater than in Montagu's harriers, difference between the sexes in the duration of molt is related to the interval between shedding feathers, not the time that each individual feather takes to grow to its full extent (Newton and Marquiss 1982).

Both sexes differed slightly in the order which secondary and tail feathers were molted. Females molted secondaries 2 and 4 before finishing the tertials, whereas molt of the tertials proceeded at a faster rate in males. Additionally, males molted the outermost tail feathers before any other. The adaptive reasons (if any) for these different strategies are unclear, and the apparent pattern might be an artifact of sample size used in our study.

Yearlings do not usually have the same energetic costs of adults, and their plumage is usually of poorer quality. Thus, it would be expected that they start replacing their flight feathers earlier than adults. This has been found to be true of yearling sparrowhawks (Newton and Marquiss 1982), cap-

tive goshawks (Reading 1990), and pallid harriers (*Circus macrourus*; Piechocki 1955). In this study, yearlings did not appear to start molt significantly earlier than adults. This again may have been due to sample size limitations; however, younger birds are less experienced hunters than adults, so they may be under higher nutritional stress, especially individuals that have undergone spring migration. Some yearlings summer in Africa and apparently they replace remiges faster than birds returning to the breeding grounds (D. Forsman, in litt.). In this study, the highest PMS among yearlings early in the cycle were shown by females that bred (shot while incubating), possibly because they were fed by males, and were in better condition than other yearlings (of either sex) that had to hunt for themselves. On the other hand, yearlings seemed to complete molt before adults although the differences were not significant. Second-yr males, which are probably nonbreeders (given that most males do not start breeding until the third year; Cramp and Simmons 1980), appeared to finish molt before older males. This suggests that nonbreeding birds molted at a faster rate. Alternatively, different age groups might have different migration strategies, which in turn might influence molt if yearlings migrate at a slower rate. If young birds make more stopovers to feed, they might be able sustain a higher rate of molt in flight feathers as has been shown in steppe buzzards (*Buteo buteo vulpinus*; Gorney and Yom-Tov 1994).

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